On the perspectives of populations of the rare plant species Phyteuma nigrum

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SUMMARY

In this thesis effects of habitat characteristics and population size on the perspectives of populations of the rare perennial and self-incompatible plant species *Phyteuma nigrum* F.W. Schmidt (Campanulaceae) were studied. Two approaches were applied: the declining population approach and the small population approach. *Phyteuma nigrum* has been rare for a long time in The Netherlands. The last decades, however, the number of populations in The Netherlands, as well as the number and sizes of populations in the Drentse Aa area (53°N, 6°40'E), where the largest Dutch population is situated, have declined. First, the possible causes of the rarity and decline of this species in this area, at the northwestern limit of the species geographic range, were investigated. The next step consisted of the assessment of the consequences of population size and (changes in) environmental conditions on population perspectives by comparing populations of different sizes for several fitness components.

An analysis of the changes in species composition and cover percentages of associated species from 1973 to 1991 at sites with *P. nigrum*, revealed that possible agents of the decline of *P. nigrum* were acidification, impoverishment of the soil and increasing wetness. Acidification was most directly related to a decline in local abundance of *P. nigrum*. Analysis of three transects in hay meadows with different abundances of *P. nigrum* confirmed that *P. nigrum* is found at soils with relatively high pH-values and moderate groundwater levels. Therefore, it was concluded that superficial acidification can be an important cause of decline in the shallow rooting *P. nigrum* in this area.

In two experiments with different nutrient treatments, seedlings of three different-sized populations showed the same yield pattern: yield increased with population size in progeny groups from these three populations. However, progeny from another small population performed remarkably well. In this case, population size alone could not explain sufficiently the differences between population performances. Maternal plants had a very significant effect on variation in fitness parameters in both experiments. No clear relationship between the amount of phenotypic variation and population size was found in these experiments, but in general the largest population gave the lowest CV-values. Responses of maternal half-sib families (the change in mean value of a fitness parameter from nutrient poor to nutrient rich conditons) were lowest in the smallest, intermediate in the medium-sized, and highest in the largest population. Therefore, it was concluded that the ability to perform well under different conditions was positively related to population size. It was argued that, perspectives for all populations (irrespective of population size) could be affected by the random elimination of individuals, although theoretically demographic stochasticity is expected to affect the extinction process only in populations

with an effective size of 50 or less.

The picture that emerged from a reciprocal seedling transplant experiment was that survival and performance of surviving individuals were determined to a large extent by site effects, and that population size effects were only of additional importance for the performance of surviving individuals. Small population seedlings survived relatively well under favourable habitat conditions. Again, this was an indication that population size alone is not a good predictor of progeny performance in *P. nigrum*. Survival and performance of transplanted seedlings were better at the large population meadow site than at the small population road verge site. This confirmed the assumption that population size at this moment may reflect the suitability of local habitat conditions for *P. nigrum* quite well. The fitness advantage, caused by a relatively high survival of large population offspring at the meadow site, was increased by the better performance of surviving plants of this population compared to offspring from smaller populations. In contrast, the fitness disadvantage, caused by a relatively low number of surviving seedlings from the small population at the road verge site, was increased by the higher chance of winter mortality of seedlings of this population compared to offspring of larger populations.

The effects of population size and flowering phenology on components of reproductive success in *P. nigrum* were investigated in two consecutive years (4 and 7 populations, respectively). Rough estimates of the total population seed output showed that, even if a seed would have the same chance of germination and of establisment in small and large populations, the chance of one successful establishment in the largest population was ca. 500 times higher than in the smallest population. Because of the fact that seedlings were less likely to survive at a small population site than at a large population site, it was concluded that the increase in population size of small populations was more likely to be seed limited than that of the large population. Artificial pollinations carried out under controlled conditions with offspring from 3 different-sized populations (Parweg, Meander and Poplaan) confirmed that *P. nigrum* is highly self-incompatible. This experiment also showed that the potential for siring and producing seeds was still good in these 3 populations, irrespective of population size. A highly significant effect of the maternal plant on number of seeds was found, but pollination with a related pollen donor (biparental inbreeding) only reduced seed production significantly in the two largest populations. This result could have been explained by assuming that all individuals in the small Parweg population were in fact related. However, if this would have been true, then seed production in this population should have been enhanced by between-population crosses, which was not found. Under natural conditions, low mean seed set and high between-individual variation in seed set in the two smallest populations (Elsbroek and Taarlo Oost) showed that the deposition of self-pollen, biparental inbreeding or the loss of incompatibilty alleles, could have played a role in these populations. A lack of bumblebee visits to flowering plants growing in very low densities (throughout the flowering period in very small populations and at the end of the flowering period in larger populations as well), could have caused a low seed production in the two smallest populations and at the end of the flowering period in one small, one medium-sized and one large population. It was concluded that reproductive limitations in *P. nigrum* were likely to occur only in very small populations (N of less than 20 flowering individuals) or at low densities very late in the flowering season.

Throughout the thesis, three populations were studied more intensively than other populations: the small Parweg population, the medium-sized Meander population, and the large Poplaan population. The relatively poor performance of progeny groups of the small population in several experiments, combined with the apparently unsuitable habitat conditions at the home site of the small population, indicated that the potential for an increase in population size could be limited in this population. Nevertheless, occasionally, this population did show good performances, shown by a high reproductive output in 1990 and by a high seedling survival in the meadow site after transplantation. Progeny from the medium-sized population performed relatively poor in two transplant experiments and had relatively high CV-values for components of reproductive success compared to other populations. The large population did not always show the largest mean values for components of reproductive success, but performance was relatively constant and progeny performance was good (mostly significantly better) in all experiments. Low intra-population variation within years and low between-year variation in reproductive output and seedling performance (consistently high mean values) in this large population lead us to conclude that this population has good perspectives for short-term survival if local habitat conditions can be maintained. However, both the small Parweg population (high between-year variation in reproductive output, poor performance of seedlings) and the medium-sized Meander population (high between-individual variation in reproductive output, high between-year variation in performance of seedlings) are more likely to become senescent or decrease in size in the near future.

The implications of the results obtained in this thesis for the conservation of populations of *P. nigrum* in the Drentse Aa area were discussed. It was concluded that for *P. nigrum* moist (but not too wet) conditions and relatively high pH-values of the upper soil were important for the long-term perspectives of populations within the Drentse Aa area. However, it was noted that the possibilities for the long-term maintenance of these conditions were probably limited within hay meadows in the middle course area, since high pH-values are usually associated with very wet conditions. If the upper soil becomes acidified, even the largest populations might become extinct. The acidification of the upper soil could probably already have started in the area where the Poplaan Zuid transect was located. The maintenance of the meadow habitat type (edges of ditches) seemed dependent on both direct management (cleaning of shallow ditches) and indirect management (the maintenance of a strong groundwater influence). The maintenance of the stream bank habitat, the second main habitat type, was considered less difficult than the maintenance of the "ditch" habitat type. For both habitat types, however, the maintenance of the regional groundwater flow pattern was considered to be of utmost importance to provide long-term perspectives for large populations of *P. nigrum*.

Since reproduction was seriously affected in very small populations only, it was concluded that a minimum viable population should at least consist of 20 flowering individuals. However, even a population of 300 flowering individuals showed reduced individual fitness and only offspring of the largest population (> 1000 flowering individuals) showed a consistently high performance. Population size alone could not always sufficiently explain differences in progeny performance, and habitat characteristics did affect progeny performance seriously. Therefore, it was argued that estimates for minimum viable population sizes of *P. nigrum* should take local habitat characteristics into account. To assess perspectives of populations of *Phyteuma nigrum*, the combination of the declining population approach and the small population approach proved to be fruitful.